No. 6 — *On a Taxonomic Puzzle and the Classification of the Earthworms*[1]

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The puzzle is provided by earthworms belonging to an undescribed species, secured by an anonymous collector at an unknown site. Fortunately, a dozen specimens, more than have been studied in many species, are available. These worms must have been unusually well preserved originally, but their present condition calls attention to the necessity of discovering ways of preventing deterioration in museum material.

The difficulties encountered in trying to place the new species in the "classical system" of the Oligochaeta called attention once more to the need for a critical examination of the nature of that classification. This is undertaken in the discussion.

DESCRIPTION

External characteristics. Length, 450-500 mm. Diameter, 7-8 mm. Pigment unrecognizable (alcoholic preservation probable). Prostomium epilobous, tongue short and open (3 specimens) or closed (1 specimen), combined pro- and epilobous (1 specimen), seemingly proepilobous (1 specimen), indeterminable (6 specimens). Setae, eight per segment and present from ii, rather closely paired, ventral couples (and also follicle apertures) of xvii-xix usually unrecognizable, in front of clitellum *AB* a trifle smaller than *CD*, *BC* $<$ or $>$ *AA*, *DD* ca. $=$ ½C. Nephropores unrecognizable and microscopic. First dorsal pore at 8/9 (2 specimens), ?9/10 (4 specimens), 9/10 (6 specimens).

Clitellum, saddle-shaped, reaching ventrally to *B*, intersegmental furrows obliterated, dorsal pores not occluded and presumably functional, setae probably present but deeply retracted and exceedingly difficult to recognize, on (xiii?)xiv-xix(xx? 1 specimen), (xiii?)xiv-xx (1 specimen), xiv-xix (2 specimens), xiv-xx (8 specimens).

[1] The discussion of classification is from a manuscript, written during tenure of a John Simon Guggenheim fellowship, 1952-1953, but with such minor changes as were required to bring it up to date, March 1959.

Spermathecal pores minute, superficial, at or slightly median to *B*, slightly in front of or on segmental equators, two pairs, in viii-ix. Female pores at or slightly lateral to *A*, about equidistant from 13/14 and eq/xiv or slightly nearer 13/14. Male pores minute (each on a very small tubercle at eq/xviii?). Prostatic pores minute, two pairs, in *AB* at eq/xvii and eq/xix. Seminal grooves nearly straight or slightly concave laterally, between eq/xvii and eq/xix, at or slightly median to *B*, deep and wide (i. e., not mere linear furrows), containing male pores and with prostatic pores at the ends. Each groove is within a protuberant, longitudinally elliptical area (of epidermal thickening?). A deep slit-like crease at mV crosses all of xvii-xix, reaching into xvi (2 specimens), through xiii (1 specimen).

Genital markings unpaired, transversely placed, presetal, in *BB*, on xx and xxi (12 specimens). Additional markings of the same sort as follows: on xv-xvi (2 specimens), xvi (1 specimen), xv, xvi and xxii (1 specimen), xvi and xxii (3 specimens). A central portion of each marking is greyish and translucent.

Internal anatomy. Septum 5/6 funnel-shaped, slightly strengthened and translucent, 6/7-10/11 thickly muscular. Longitudinal muscle band at mD distinct from level of first dorsal pore or pore-like marking, unrecognizable anteriorly. Pigment unrecognizable in body wall except at mD, the muscle band, in one or more scattered segments or through several consecutive metameres, often dark red. The subesophageal mesentery in x-xiii seems to be slightly strengthened.

Gizzards well developed, lined with thick cuticle, two, in v-vi (12 specimens). Cuticular lining continued from gizzards through viii or ix (at least?). Esophagus widened and moniliform in xi-xiii where there are (internally) closely crowded rather lamelliform but low and vertical ridges as well as a bifurcated ventral typhlosole (12 specimens). Intestinal origin in region of 15/16. Intestinal typhlosole lacking (?).

Dorsal blood vessel single, complete, bifurcating under the brain, the branches passing ventrally and uniting over the subesophageal ganglion to become the ventral trunk. Latter also complete, with two pairs of branches between 4/5 and the anterior bifurcation. Extra-esophageal trunks filled with blood anteriorly and traceable forward into ii, posterior portions unrecognizable, median to hearts. Supra-esophageal trunk present

in ix-xiii. Subneural trunk lacking (?). Hearts of x-xiii apparently latero-esophageal though blood is lacking in filamentous branches to the dorsal trunk. Last hearts in xiii (11 specimens). Hearts of ix-vi (all easily traced to ventral trunk), lateral. Hearts of v may pass to ventral vessel on one or both sides but usually are not traceable to that trunk. Brain in ii or in iii.

Excretory system meronephric. Astomate micronephridia cover body wall in (ii?)iii-iv. At least from iv the number per segment decreases, to 40-50 in x, the small astomate tubules in the latter metamere and posteriorly in a row just in front of the septum and from region of *A* nearly to mD. Several nephridia are crowded together at the median end of a row but as far back as tubules are distinguishable all are astomate.

Holandric (12 specimens). Male funnels, and presumably also testes, free in x-xi. Male deferent ducts slender, becoming unrecognizable shortly behind funnel septa and after passing to parietes. Seminal vesicles medium-sized or smaller, finely acinous, low down in coelomic cavities, two pairs, in ix and xii. Prostates medium-sized, flat discs, racemose,[2] two pairs, each usually extending through three segments, usually three to six levels behind xvii or xix with their ducts passing anteriorly through septal perforations, occasionally in xvi-xvii and xviii-xx, once seemingly confined to xvii and xix but bulging septa far posteriorly. Duct slender but probably muscular, 4-6 mm. long.

Spermathecae fairly large but not reaching dorsal parietes, always bound to anterior septum of their segment by fairly strong tissue from which the ectal half of the duct is free. Duct slender, probably muscular though sheen no longer recognizable, slightly widened entally but an appearance of even greater widening is due to presence of one or two very short loops bound closely together. Seminal chamber ellipsoidal, sessile vertically on entalmost portion of duct into which it opens entally by a single aperture.

GM glands represented by clusters of several very small spheroidal bodies, the clusters always covering the parietes over sites of genital markings except in two specimens with least obvious clitella and in which the little glands may not have

[2] Without a central lumen. (Sections have been deposited in the Museum of Comparative Zoology.)

reached definitive size. (These glands, in some of the specimens, are not easy to distinguish from the nephridia.)

Ventral follicles (*a* and *b*) of viii, ix, xvii and xix, completely buried within the parietes, contain setae that are much slenderer and shorter than those of neighboring segments. Shafts of these smaller setae are straight and taper ectally but not to a sharp point. Ornamentation on the penial setae, as those of xvii and xix presumably should be called in spite of their small size, is of several (four?) longitudinal rows of four or five excavations. Each pit is long, narrow, deepened entally where its floor is finely nodose. Excavations on the copulatory setae (*a* and *b* of viii-ix) are of the same sort but more numerous, in longitudinal rows of seven to nine. Ectalmost pits are closer to the tip than on the penial setae but ends of copulatory setae may have been subjected to more erosion. Ventral setae of xviii appear to be lacking as their follicles were not found.

Reproduction. Irideseence on male funnels of each specimen (including the aberrant one) proves that sperm had been matured. A similar iridescence in the spermathecal seminal chambers of each worm shows that copulation had taken place. Reproduction, accordingly, is assumed to be sexual and biparental.

Ingesta. The gut of each worm is filled with a sort of humus in which plant parts or tissues are not distinguishable. Little or no sand and clay is present. These worms appear to be discriminating feeders.

Abnormality. Organs of right side belonging in viii-xix are (1 specimen) one segment anterior to their normal location: spermathecal pores on vii-viii, female pore on xiii, prostatic pores on xvi and xviii, last heart in xii, testes in ix-x, seminal vesicles in viii and xi, etc. The clitellum is on xiii-xx on both sides. Both hearts of ix are lateral.

Presumably a mesoblastic somite at the seventh level (or anteriorly?) was aborted early in development.

Remarks. The worms may have been quickly killed and properly preserved. Unfortunately, however, subsequent care had been lacking and all are macerated, especially from region of xxiii to hind end. The size of properly preserved, contracted specimens is estimated to be between 150-250 x 9-10 mm. Locations of prostatic pores were confirmed by dissecting prostatic

ducts out of the body wall. Location of male pores, inasmuch as vasa deferentia cannot be traced, requires confirmation. No evidence was found to indicate junction of those gonoducts with the prostatic ducts. Some of the seeming variation in antero-posterior extent of the clitellum may be due to incomplete development as the tumescence, in several of the specimens, is slight. The intestinal wall had been reduced to a transparent slime in which caeca and supra-intestinal glands might not have been recognizable. A typhlosole, if present, should have been distinguishable as a lamella of slime extending down into gut contents. When a typhlosole is absent supra-intestinal glands usually are lacking. Complete relaxation of the esophageal valve in each specimen, along with the maceration, obviated determination of site of intestinal origin which is unlikely to be variable, except as a result of some aberration in embryonic development.

Characterization of excretory organs behind xxx is impossible. If nephridia are exonephric throughout the body all may be small and astomate as in *Octochactoides*, or the medianmost on each side of some posterior segments may be larger (as in various octochaetine genera) and provided with a preseptal funnel. Although less likely perhaps, some or even all of the micronephridia, along a major posterior portion of the axis, may be enteronephric and stomate. Presence in posterior segments of one to several pairs of large, stomate, enteronephric nephridia is not anticipated.

Uniformity in number of prostates and in relation of their external apertures to the male pores among so many specimens, even including one that is aberrant, seems to warrant an assumption that the arrangement of the male terminalia is characteristic of the species to which these worms belong. An "acanthodriline" arrangement of racemose prostates has been unknown hitherto and requires, in the Oligochaeta where a single character rarely is diagnostic at any taxonomic level, erection of a new genus.

Although diagnosis is assured, determination of relationships must await much more adequate description of digestive, vascular and excretory systems than is permitted by available material. Some generic characters cannot, of course, be recognized when only one species is known. Intestinal origin, for instance, is uniform in some genera, possibly even throughout one

family (Lumbricidae), but is subject to individual variation in the Moniligastridae. A typhlosole is lacking in some genera and even throughout one family (Moniligastridae), but is now known to be absent only in some of the species of several genera. Number of gizzards is uniform in some genera and subfamilies, but in the Moniligastridae is subject to individual variation. Andry, in spite of the reliance placed on it in the classical system, does vary intragenerically, sometimes even intraspecifically. Hence, the definition below is tentative. In fact, any generic definition must be considered liable to revision, at least until all species have been satisfactorily described. A definition certainly does not become sacrosanct through publication in a thick monograph. Yet species, genera, even one family, have been erected because of unimportant difference from one or more characters as stated in definitions.

Taxonomically important characters that are unknown or in need of confirmation, in accordance with previous practice, are indicated below at specific as well as generic level.

Genus EXXUS gen. nov.

Definition. Quadriprostatic, prostates racemose and of pheretima sort but with ducts opening externally at equators of xvii and xix. Male pores (in seminal grooves that extend from eq/xvii to eq/xix) at eq/xviii (?). Setae, eight per segment and paired (throughout?).

Gizzards in v-vi. (Intestinal origin in xv?) Calciferous glands (typhlosole, intestinal caeca and supra-intestinal glands?) lacking. Vascular system with complete (single) dorsal trunk, with extra-esophageal trunks median to hearts, with a supra-esophageal trunk in ix-xiii but without a subneural(?), (lateroparietal trunks?), and with latero-esophageal hearts in x-xiii. Excretory system meronephric, nephridia astomate and exonephric (throughout or enteronephric in iii-iv?), massed on parietes in iii-iv, but posteriorly — on each side of each segment — in a transverse row, extending from *A* nearly to mD just in front of the septum.

Type species. Exxus wyensis sp. nov.

Precis of E. wyensis. Quadrithecal, spermathecal pores minute, superficial, two pairs, at or slightly median to *B*, on or

slightly in front of segmental equators, in viii-ix. Female pores at or slightly lateral to *A*, about midway between 13/14 and eq/xiv. Male and prostatic pores minute and superficial. Genital markings unpaired, in *BB*, presetal, on xx and xxi, often with one or more similar markings in some of xv-xvi, xxii. Setae, rather closely paired, *DD* ca. = ½C (throughout?), ventral setae of xviii lacking at maturity (?), *a* and *b* of xvii and xix (penial) as well as of viii-ix (copulatory) concealed in small follicles within parietes and ornamented ectally by several longitudinal rows of narrow pits that are deeper entally and there with a nodose floor. Clitellum, saddle-shaped, on xiii, xiv-xix, xx. First dorsal pore at 8/9 or 9/10. Prostomium, epilobous(?). Pigmentation, red(?). (Segments?) Size, 150-250 by 9-10(?) mm.

Septa 6/7-10/11 thickly muscular. Atyphlosolate(?). Intestinal origin in xv (?). Holandric. Seminal vesicles, small, acinous, two pairs, in ix and xii. (Ovaries fan-shaped and with numerous egg strings?) Spermathecae medium-sized, each with a vertically ellipsoidal seminal chamber sessile on duct near ampulla and opening into duct entally. GM glands small (composite?), numerous, nearly covering parietes over sites of genital markings.

Reproduction. Presumably sexual and biparental.

Distribution. Unknown.

DISCUSSION

One important part of the puzzle mentioned in the title is finding a place for the new genus in the "classical" system of the Oligochaeta. That classification, as presented in the tenth volume of Das Tierreich (Michaelsen, 1900), was regarded as "a triumph of arrangement which brought order into confusion and constituted a remarkable advance in our understanding of the group" (Stephenson, 1930, p. 716), more especially because of the "clear and logical division into subfamilies, *on a phylogenetic basis*, of the large family Megascolecidae" (italics not in original). Few of the various modifications proposed during the last half century (cf. Table 2 and subjoined notes) have been universally acceptable. Accordingly, the classification in the latest monograph on the order, The Oligochaeta (Stephen-

son, 1930), is recognized, for greater convenience in the ensuing discussion, as a currently terminal stage in development of the classical system.

The new genus clearly belongs in the Megascolecidae, where the male genitalia appear, from the definitions, to be of considerable taxonomic importance. Arrangement of the terminalia in *Exxus* is "purely acanthodriline,"[3] i. e., there are two pairs of prostates having apertures at equators of segments xvii and xix but with the male gonoducts opening typically to the exterior on xviii midway between the other pores. Acanthodrilin terminalia are allowable in the Acanthodrilinae, Ocnerodrilinae, Diplocardiinae and Octochaetinae, but the genus cannot go in either of the first three subfamilies where, by definition, prostates must be tubular. Inclusion in the Octochaetinae at first does seem permissible as prostates are not mentioned in the definition. The omission probably was unintentional as all genera do have tubular prostates and Michaelsen (1900, p. 319) did specify "Prostaten schlauchförmig." Glands of the racemose kind found in *E. wyensis* are permissible in the last remaining subfamily where the prostates are "tubular or racemose (pheretima prostates)." Those organs, however, by definition, are limited to one pair "with each prostatic duct uniting with the vas deferens of the same side and opening in common with it (except in *Diplotrema*)" on xviii. The exception provides no loophole as prostates in *Diplotrema* are tubular and their pores, though discrete, are on xviii, close to the male apertures.

Erection of a new subfamily for a single species, in spite of all those difficulties, seems unwarranted, in which case modification of the classification becomes necessary. Any *ex tempore* changes, solely for accommodation of one troublesome form, might later prove to be as ill advised as some of those proposed during the last forty years. Accordingly, a review of the entire classical arrangement of the Megascolecidae seems advisable and this can begin appropriately with an examination of family and subfamily definitions.

3 Various patterns of morphological organization long have been characterized as lumbricine, microscolecine, etc., though none are diagnostic of the named subfamilies and some are common to several families. The adjective designating pattern is hereinafter distinguished from that for a subfamily by omission of the final vowel.

Megascolecidae (*cf.* Stephenson, 1930, p. 818). The definition comprises eight sentences. One and parts of two others are unqualified. "Setae sigmoid, single pointed," correct, but equally applicable to all earthworm families and some Microdrili. "One pair of male pores," not universally true throughout the family, as two pairs of male pores are present in species of *Hoplochaetella*, and, in several subfamilies, parthenogenetic strains have no male pores. "One pair of ovaries in xiii.," true of most families of earthworms but here inadequate. Ovaries in one genus, possibly two, are always in xii and at least one species (of *Diplocardia*) has two pairs of ovaries in xii-xiii. Other parts of the definition are qualified, by "usually," "rarely," exceptions or alternatives. One such statement, "Two pairs of testes in segments x and xi, or one pair only, in x or xi" is equally applicable to the Eudrilidae, Glossoscolecidae, Lumbricidae and the microdrilin Haplotaxidae, but is actually inadequate for the Megascolecinae which contains one genus, possibly two, with testes in ix and x. Each of the characters mentioned in the definition is found in various other families, hence none (at least as stated) is diagnostic.

Acanthodrilinae (*idem*, p. 820). Two statements are unexceptional: "Meganephridial. Prostates tubular." Neither is diagnostic, tubular prostates being common in each of the sister subfamilies as also are "meganephridia." The latter term, in its literally descriptive meaning, has no taxonomic value at family or subfamily levels. Redefining the word is unnecessary, as an accurately descriptive term, holonephric (or holonephridial), is available. Other characters mentioned in the definition are qualified by "mostly," "more or less," or are in pairs of alternatives, sometimes even with qualifications. None of the characters, with or without qualification, is diagnostic, being equally applicable to sister subfamilies, other families and even some Microdrili.

Megascolecinae (*idem*, p. 828). Two characters here also are stated without qualification: "Male pores on xviii. Prostates one pair." Neither is diagnostic, each being applicable at least to some portion of the other subfamilies. Although male pores may sometimes be on xviii in other families they are by no means universally so in the Megascolecinae. In one genus, perhaps two,

the pores are always on xvii, in another they may be on xvii, xviii, xix or xx; in *Plutellus* they may be on xviii, xix or xx. Number of prostates in some megascolecine species is subject to individual variation. In *Pheretima posthuma* as many as three pairs have been found. Other statements in the definition, even with all their qualifications are inadequate. "Usually one gizzard in front of the testis segments, sometimes two or three, exceptionally none," should read somewhat as follows: Gizzard lacking, single, in a single segment or in a space formed by abortion of one or more septa, or double or triple, in front of testis segments, or one in front of testis segments and several more behind. Similarly, "Spermathecal pores, if present, one to seven pairs, in front of testis segments" should be: Athecal or thecal and then spermathecae usually in front of testis segments, rarely in or even behind those segments, pores unpaired, paired, in pairs of pairs or in pairs of groups.

Octochaetinae (*idem*, p. 841). No statements unqualified and no character diagnostic. The prolixity of one characterization, "Excretory system of meganephridia along with micronephridia or micronephridia alone, the latter never having the form of sacs" can be avoided, with considerable gain in taxonomic accuracy, by use of three words: Excretory system meronephric.

Diplocardiinae (*idem*, p. 849). Two unqualified statements. Both are applicable to sister subfamilies, one to other families. No character is diagnostic.

Ocnerodrilinae (*idem*, p. 852). Three unqualified statements, two being the same as in the definition of the Diplocardiinae; the third is "Meganephridial." Characterization of the calciferous section of the gut should, strictly speaking, exclude an important section of the subfamily containing two of Stephenson's genera. This was, however, avoided by interpreting certain microscopic spaces in the esophageal wall as vestiges of paired extramural calciferous glands.

These definitions, which contain no diagnostic characters, do not define but merely list some of the more obvious or better known structural diversities of a group, and now appear to have resulted from construction of the classification "on a phylogenetic basis." Morphological changes that mean anything from the evolutionary point of view, according to Stephenson, are

few. We know, continues the argument, which characters are primitive and which are secondary. The principal pairs or groups of primitive-secondary characters are: One gizzard — multiple gizzards. Lumbricin setae — perichaetin setae. Holonephric — meronephric. Tubular prostates — racemose prostates. Acanthodrilin genitalia — microscolecin, megascolecin, balantin genitalia. Characters of lesser importance are: Calciferous glands absent — calciferous glands present. Holandry-proandry, metandry. Hologyny-progyny, metagyny. Those are just the characters by which megascolecid genera were defined. Genera so characterized could then be arranged serially in evolutionary lineages of a mother-daughter-granddaughter sort. The amazing result of the filiations was a phylogenetic tree with all of the stages in the evolution of the subfamilies still available for investigation, "a living paleontology — as if students of the Equidae had all the stages in the ancestry of the horse alive before them today." Correctness of the filiations was "proved" by forms that were found to be transitional between mother and daughter genera.

Since anatomical changes that amount to anything from an evolutionary point of view are so very few, convergence is frequent in the Oligochaeta. Perichaetin setae, for instance, have appeared in the Acanthodrilinae, Octochaetinae, Megascolecinae and in the Glossoscolecidae, meronephry in various megascolecine lines of descent as well as in the Diplocardiinae and the Octochaetinae, calciferous glands in all megascolecid subfamilies (even including the Acanthodrilinae) and also in the Glossoscolecidae and Lumbricidae. Necessarily, convergent genera resulted. The diplocardiine *Monogaster* of tropical Africa was distinguished from the octochaetine *Octochaetus* of Pacific areas only by its distribution as the "definitions of the two genera are the same." Similarly, distribution distinguished the acanthodriline *Udeina*[4] of South Africa from the megascolecine *Plutellus* of Pacific areas. Nor is the convergence always as simple taxonomically as in those two instances, for genera may be polyphy-

[4] The terminalia were erroneously characterized and are not megascolecin as Pickford (1937) later discovered. The two species of *Udeina* may have arisen independently from different species groups of the acanthodriline *Parachilota*, according to Pickford (1937), by changes that now appear to be relatively unimportant and of dubious value for generic distinction.

letic. *Megascolex*, the best example, evolved from *Perionyx*, *Spenceriella* and two different sections of *Notoscolex*. In that case as well as in others, anatomy permitted recognition of diverse origins but how much polyphyly would remain morphologically or geographically undetectable was beyond estimation. Acquisition of further data occasionally might enable resolution of a fraction of the polyphyly, but usually Stephenson seems pessimistic about taxonomic boundary lines. They are "bound to be merely arbitrary" (1923, p. 193), and "since all such lines are arbitrary interruptions in the record of a continuous process" (1930, p. 833) it does not matter very much where they are drawn. Convenience, presumably of the systematist, was the criterion employed in various cases.

No comment seems necessary as to sequence in some of the pairs or groups of primitive-secondary characters. The acanthodrilin male terminalia, however, may not always have been ancestral to the other kinds and, like some of them, may have been derived from a more ancient (and possibly less uniform?) arrangement. The prostate sequence certainly requires consideration. The pheretima kind lacks a central lumen throughout and the duct may even branch outside of the gland. Supposedly intermediate sorts of racemose prostates, having a central lumen into which more or less definite lateral canals open, really are tubular. The pheretima prostate develops ontogenetically (Stephenson and Ram, 1919) from peritoneal proliferation and acquires an external aperture by growth outward through the body wall. Tubular prostates, on the contrary, are epidermal invaginations (Pickford, 1937) — as can be seen in dissections of juveniles. Gradual evolution of an ectodermal ingrowth into a mesodermal outgrowth, especially in animals with a determinate embryology, is difficult to visualize and now appears improbable. Megascolecin terminalia, those in which male gonoducts unite with the ducts of a single pair of ectodermal or mesodermal prostates to open externally, through one pair of male pores on xviii, accordingly provide another but hitherto unrecognized example of convergence. The "arbitrary" selection of such terminalia as the distinguishing character of a subfamily produced an otherwise undefinable and markedly polyphyletic group.

Delimitation of other megascolecid subfamilies, it may here be noted, was no more fortunate. Selection of a form with extra-

mural and paired calciferous glands in ix and x as the initial stage in ocnerodriline evolution necessitated deriving the unpaired condition in *Curgiona* and *Gordiodrilus* by fusion midventrally of paired sacs, and interpreting microscopic spaces in the esophageal wall of Indian genera as rudiments of retracted extramural glands. Both derivations seem improbable. The Diplocardiinae, in which the initial evolutionary stage was duplication of the gizzard, has gradually disappeared (*cf.* note 6, Table) into the two remaining subfamilies. The more recent, the Octochaetinae, with endemic genera in New Zealand, India, Africa and the Americas, now appears (Gates, 1958b) to be polyphyletic. The older Acanthodrilinae comprises the phylogenetic "brushwood" that was left over from delimitation of sister subfamilies. The group does seem to have some little common anatomy, but the wide discontinuities in its distribution (New Caledonia, Australia, New Zealand, the Americas, Africa, Madagascar, Cape Verde and Subantarctic Islands), especially if earthworm evolution is limited (Stephenson, 1930) to the Tertiary and Quaternary, suggests polyphyly.

Delimitation of megascolecid genera in the classical manner has proved to be even more unsatisfactory. On various occasions, since 1900, Michaelsen himself shifted generic boundaries back and forth, or abolished them. As for the Acanthodrilinae, Benham could not agree with Michaelsen, and after her study of the group Pickford differed from both of them. On megascolecine demarcations, Stephenson disagreed with Michaelsen, and Gates could follow neither. In the Ocnerodrilinae, Michaelsen's treatment of boundaries that left *Gordiodrilus* another waste-basket of phylogenetic "brushwood" has been questioned (Gates, 1942). More recently (Gates, 1957b) validity of some hitherto undisputed demarcations was challenged. In the Octochaetinae, several lines (Gates, various publications) had to be changed, and now (Omodeo, 1958) two genera have been resurrected (as well as a subfamily) from synonymies, where they had been buried for 60 years. Many more changes can be expected and especially — if the past provides any basis for prophecy — whenever a group is studied by another person. Accordingly, further consideration of individual areas of controversy may well be left to the future.

Hitherto undisputed boundaries do, however, require some comment. Andry, for instance, is not mentioned in definitions of octochaetine as well as most megascolecine and diplocardiine genera. The three standard characters had been found to have taxonomic value only at species level. All acanthodriline and most ocnerodriline genera, on the contrary, are defined by andry which also has considerable importance in the basic phylogenetic esoteries. Even supra-generic groups, in the Acanthodrilinae, are defined by andry. *Nematogenia,* hitherto meroandric by definition, now includes (Gates, 1957b) a holandric species. Holandry and marked hyperandry each have been found in many individuals of a species of *Pheretima,* holandry and anandry in another species of that genus. Holandry, proandry, metandry, hyperandry, anandry, all have been found in worms with genital and somatic anatomy that require the lot to be in one and the same species. Individuals, if not also species, sometimes are morphologically holandric though functionally meroandric.

Standard characters of the male terminalia, in six non-megascolecine genera, were allowed taxonomic value only at species level. Other genera in the Acanthodrilinae, Octochaetinae, Diplocardiinae and Ocnerodrilinae, on the contrary, were delimited from each other by their terminalia to which again considerable importance is attached in phylogenetic esoteries. *Microscolex georgianus* is supposed to have acanthodrilin terminalia, but the posterior pair of prostates fails to develop in an occasional individual which is then microscolecin. Aprostatic individuals have been found in one species of *Diplocardia.* Variation as to number and segmental location of prostates has been found in species of several ocnerodriline genera. More data of similar sorts and from various subfamilies can be expected when efforts are made to study individual variation on a significant scale.

All of the male genitalia now appear to be liable to rapid or abrupt and perhaps macromutational modification. Accordingly, status of genera presently distinguished from each other by andry and/or characters of the terminalia only is dubious. Such genera will have to be united if good evidence to the contrary — preferably from somatic anatomy — is not forthcoming.

The least departure from the very common and ancient lumbricin arrangement of setae constitutes (as Stephenson maintained) a definite and natural line of demarcation. But, of what taxonomic value? The change has been made in one glossoscolecid subfamily and probably on more than one occasion in each of the megascolecid subfamilies except the Ocnerodrilinae. In every instance the extra setae presumably first appeared in individuals of one or more species of a good (*i. e.,* natural or monophyletic) genus, as now seems to have happened in the glossoscolecine *Periscolex.* Somatic anatomy, in that taxon, must have obviated a generic division according to setal numbers. A natural boundary in an evolutionary process can then be placed arbitrarily in a classification as would have been the case if *Periscolex* had been split in the same manner as some of the Megascolecinae. Such arbitrariness now seems to have been responsible for part of the much discussed megascolecine polyphyly. Investigation of somatic anatomy is expected to show that *Megascolex,* as well as several other megascolecine taxa, are quite unnatural congeries, resolvable into morphologically homogeneous and monophyletic genera.

The digestive system provided two classical sets of standard characters. One of the organs, the gizzard, is not homologous throughout the Oligochaeta. Much of the argument over that structure early in this century was about taxonomic value of presence or absence of a single esophageal gizzard. Intermediate stages, characterized as weak, feeble, rudimentary and vestigial, had been found where they were not expected. Agreement that presence or absence is unreliable as a generic character was nearly reached, but Michaelsen's opinions changed more than once. Segmental locations were not always mentioned in descriptions of species and those recorded occasionally have been thought subsequently to be wrong. Whether such errors have been responsible for any of the supposed intrageneric variation in location remains to be discovered. Transfer of a single esophageal gizzard into the segment next behind has been believed to be gradual, but for such change there is very little good evidence. That usually mentioned is insertion of a thin septum at or near the middle of a gizzard. The funnel-shaped septum has been found (in most cases that have been checked) to be inserted

behind the gizzard, though adherent to a posterior portion of it in strongly contracted specimens.

With increase in number, gizzards abruptly acquired taxonomic importance at generic and subfamily levels. The digastrin subfamily, however, was gradually disbanded, and Michaelsen seems to have concluded that a third gizzard was inadequate to distinguish *Eutrigaster* from *Dichogaster*. *Eutrigaster* was retained by Stephenson (1930), as was *Perissogaster* which, by definition, differs from *Digaster* only in possession of a third gizzard. Presence of a third pair of spermathecae, again by definition, is all that distinguishes *Didymogaster* from *Digaster*. That difference, *per se*, certainly does not warrant generic distinction as the spermathecal battery seems to be subject to nearly as rapid evolutionary modification as the male genitalia. All three genera, restricted to a small section of Australia, are distinguished from *Notoscolex*, according to their definitions, only by the multiple gizzards. An extra gizzard, by itself, scarcely seems to provide more justification for generic distinction than does the presence of an extra pair of setae. Considerable intraspecific variation in location and number of gizzards has been found in the moniligastrinae. Assumptions as to specific and generic uniformity of those characters in the Megascolecidae usually are unsupported by data obtained from more than a very few specimens. Pending acquisition of much more information, the taxonomic value of gizzard number and location (the only macroscopic characters the organ can supply) remains uncertain.

Calciferous glands were allotted a wide range of taxonomic values in the classical system. The organs, though sometimes present, are not even mentioned in definitions of Acanthodriline and Megascolecine genera. In other subfamilies the characters used in definitions are mainly segmental location and number. The latter often is erroneous. *Dichogaster*, by definition, has three pairs of calciferous glands. Yet, a group of common and widely peregrine species (Gates, 1942, 1958b) really has only one pair. *Howascolex* became even more of a congeries, after 1930, and by definition now has "Calciferous glands either as mere swellings of the oesophagus in segm. 14, with or without a slight development of the same kind in the neighbouring segments; or

well developed calciferous glands in segm. 14 and 15, or in segms. 8-11." *Diplocardia,* by definition, lacks calciferous glands, though a species was known to have one of a highly specialized sort. The North American genus provides (apparently within the limits of a monophyletic taxon) a beautiful series of evolutionary stages (Smith, 1924), beginning with absence of calciferous lamellae and ending with an intramural gland very similar to that of the better known Lumbricidae.

The standard characters of the remaining somatic sequence are meganephridial and micronephridial. Meganephridia may be holonephric, meronephric, exonephric, enteronephric, vesiculate or avesiculate, with or without a bladder-like caecum, of various sizes and occasionally smaller than some micronephridia, one to several pairs per segment or more numerous. Micronephridia may be stomate, astomate, exonephric, enteronephric with respect to pharynx or to intestine, vesiculate or avesiculate, several pairs per segment up to "forests" of hundreds. The standard characters obviously have little meaning in an important sector of somatic structure. Holonephric and meronephric have relegated the older terms to infrequent but more precise usage. They do characterize groups of genera or larger units more accurately than their predecessors, but even so they can have very little of the taxonomic value allowed the older pair in the classical system.

The first appearance of meronephry undoubtedly constitutes a natural and definite line of division in organ evolution but initially can provide no more justification for generic separation than addition of a few setae. Increased knowledge of somatic anatomy can be expected to reveal, in good genera, earlier stages of meronephry than have been recognized hitherto.

More ancient meronephric systems, as an interesting and important series of contributions by Bahl (1919-1945) shows, are organized in a variety of dissimilar ways. A somewhat different sort of organization is less satisfactorily described (Gates, 1943) because of poor preservation. Existence of other kinds of meronephric systems is indicated by the literature. For some time it has been quite obvious that dissimilarities in structure, as well presumably as in embryological development and phylogenetic evolution, are such as to require precise characterization at generic level.

Ever since Savigny (1826) amazed his colleagues by demonstrating the existence, in Paris, of many more than one species of earthworm, taxonomic descriptions have been mainly concerned with organs visible to the unaided eye or, in smaller forms, through a hand lens. A few organs, such as prostomium, setae, gizzard and segmentally paired holomeganephridia, doubtless were the structures seen in the juveniles, that often must have been examined. With increased knowledge, inability to find "segmental organs" became acceptable proof for existence of a micronephridial excretory system. Mature worms, however, provided the taxonomist a clitellum of diverse lengths, circumferential extent and location, an array of other epidermal modifications collectively designated as genital markings, genital pores in various locations, a battery of spermathecae, another of seminal vesicles permitting deduction of andry when male gonads were unrecognizable. Mature exotic material that increasingly became available, provided prostates of various sorts, as well as a bewildering variety in other genitalia. On the contrary, guts, blood vessels and nervous system may well have seemed to be tediously uniform. The diversity of genital structure was still far from complete elucidation during the period when Michaelsen (1900) was completing his masterpiece. The conclusion that "The sexual organs are the most important of all for systematic purposes" (Stephenson, 1923, p. 7) may have seemed unavoidable. Peremptory denial of evolutionary value (apparently equated in a phylogenetic classification with taxonomic value) to so much of the somatic anatomy, is unlikely to have stimulated investigation of it. Interesting characteristics of the vascular system in little known species were observed by Benham but being of "no taxonomic importance" they were not recorded. Inclusion in a taxonomic contribution of information about blood vessels and hearts in several genera of a little known family, even in 1930 seemed so unusual that it was mentioned in Stephenson's monograph.

Study of the octochaetine *Eutyphoeus* has enabled redefinition of the genus as given in the left column of Table 1. On the right, for comparison, is the classical definition (Stephenson, 1930). Descriptive characterizations, often in the past or still included in generic definitions, are listed after the distribution.

Table 1
Eutyphoeus

As now defined	*As previously defined*
Biprostatic, pores in region of *AB*, near eq/xvii. Male pores minute, near but behind prostatic pores.	Sexual apparatus purely microscolecine (conjoined male and prostatic pores on xvii).
Bithecal, pores superficial, never minute, at 7/8.	Spermathecal pores, one pair, at 7/8.
Setae paired, arrangement lumbricin.	Setal arrangement lumbricin.
Clitellum annular, on xiv-xvi, intersegmental furrows obliterated, dorsal pores occluded, setae retained.	
Septa 4/5-5/6 with muscular thickening, 6/7-7/8 aborted, 8/9-10/11 thickened, crowded together behind their normal locations, 11/12 approximated to 10/11.	
An esophageal gizzard belonging to vi in space between 5/6 and 8/9. Calciferous glands intramural, longitudinally hemi-ellipsoidal with flat faces mesially, numerous transverse vertical partitions and interlamellar spaces directly communicating dorsally with the esophageal lumen here T-shaped in cross-section, 1 pair in xii. Intestinal origin in xv. Typhlosole terminating with a series of doubly-paired supra-intestinal glands. Unpaired, anteriorly directed, small, midventral caeca one each in a number of consecutive segments in front of supra-intestinal glands.	An enlarged esophageal gizzard in a space formed by fusion of several segments.
	A pair of calciferous glands embedded in the esophageal wall in xii.
Dorsal blood vessel single. No subneural. Lateroparietal trunks from posterior end of body pass to hind ends of calciferous glands. Extra-esophageal trunks, median to hearts, pass to front of calciferous glands. Hearts four pairs, in x-xiii, last three pairs latero-esophageal.	

As now defined	*As previously defined*
Excretory system meronephric, all nephridia small, numerous astomate nephridia of iii pharyngonephric and apparently in a circumferential parietal band but attached to a tightly-zig-zagged cord, remainder of system exonephric and comprising astomate biramous nephridia which are numerous in next few segments but behind clitellum are in longitudinal ranks, the medianmost nephridium of each side behind supra-intestinal glands somewhat enlarged, saccular and with preseptal funnel.	Purely micronephridial.
Terminal portion of male gonoduct modified to function as a bulbus ejaculatorius.	
Spermathecal diverticula open into ental end of short duct.	
Metagynous.	
Distribution: Burma, from Tenasserim division and western margin of Shan plateau into the Gangetic Plain and through the Himalayas to beyond Nepal.	India, especially the Gangetic Plain.
Segments more than 150.	
Unpigmented or pigmented and then with dorsum brown, occasionally green but with no corresponding pigment recognizable.	
Ventral setae of xvii lacking or penial.	
Male and prostatic pores as well as apertures of penisetal follicles in two slight fissures, each with a superficial porophore or more or less deeply invaginate, vestibula paired or unpaired and median, sometimes with protrusible penes.	
Lateral intestinal caeca lacking, rudimentary and/or sporadic, or one pair.	

As now defined	*As previously defined*
Holandric or meroandric. Seminal vesicles in ix and/or xii. Coelomic cavity of xi gradually reduced to an annular, then a U-shaped and eventually a subesophageal testis sac. Two female pores, or right oviduct functionless or atrophied.	Holandric or metandric.

The revised definition contains no alternatives and no exceptions. Absence of variation with regard to the characters mentioned, in normal specimens, was determined (Gates, in press) from external examination and dissection of hundreds of specimens. The reproductive system, not excluding the female gonoducts, has undergone considerable modification during intragenerie evolution. The genitalia, from an evolutionary point of view, are not conservative. Much somatic anatomy, on the contrary, has remained uniform during a period in which the genus was spreading through rain-forests and semi-deserts, from tropical lowlands to Himalayan heights.

Eudichogaster, the parent genus of *Eutyphoeus* in the classical system, when redefined (Gates, 1939, 195?) with reference to more of somatic anatomy, cannot be ancestral. Phylogenetic filiation, as in the case of *Bahlia* which is more closely related to *Eutyphoeus*, is possible only through common descent from some form that is no longer extant (Gates, In press). *Scolioscolides*, at present known only from a single species originally placed in the Megascolecinae, is (Gates, 1937) still more closely related to *Eutyphoeus* by all of its anatomy than is either of the other genera. The "living paleontology" of the Indian Octochactinae has vanished.

That portion of the gut in the nine to fifteen segments between gizzard and esophageal valve of Indian octochaetines has provided a striking demonstration of the importance of previously neglected organization. Using only characters from such a short region, a key was constructed (Gates, 1958b) that identifies genera (except *Scolioscolides*) and simultaneously indicates those likely to need drastic revision. The key is based on macroscopic anatomy. Microscopic structure of the calciferous glands undoubtedly will provide still other defining characters. In a

short terminal portion of holonephridia, Pickford (1937) found macroscopically recognizable characters that could be used in defining Acanthodriline genera.

The classical *Megascolides* has marked discontinuities in its distribution: Peninsular India, the eastern Himalayas, Australia, Tasmania, and Oregon-Washington in North America. *M. bergtheili* Michaelsen 1907, of the Himalayas, is so nearly identical with the indubitably octochaetine and specialized *Eutyphoeus* that little more than the megascolecin terminalia is available to warrant even subgeneric separation. With that discovery (Gates, 1937), the single morphological distinction between the Octochaetinae and the Megascolecinae became taxonomically null and void. *M. prashadi* Stephenson 1920 and *annandalei* Stephenson 1921 are barely if at all distinguishable from the octochaetine *Eudichogaster barodensis* Stephenson 1914 which had to be separated off from the rest of the genus (Gates, 1939a) because of its somatic anatomy. *M. cochinensis* Michaelsen 1910, *M. duodecimalis* and *pilatus* Stephenson 1915, *M. chengannures* Aiyer 1929, have been transferred (Gates, 1940) also because of somatic anatomy to the octochaetine *Travoscolides*. *M. antrophyes* Stephenson 1924, known only from the holotype, unlike the other Indian species does seem to be megascolecine. Relationships, insofar as they could be determined in the circumstances, are with a local group of genera. With those discoveries *Megascolides* disappeared from the Orient.

The classical *Woodwardiella* of the Megascolecinae also has discontinuities in its distribution: India, Ceylon, Java, Australia. The Java record is due to transportation of a species from the west. Oriental species, because of somatic structure, had to be transferred to other genera including two, *Nellogaster* and *Nelloscolex*, that are not classical. Another genus, shared between Australia and South India, that is terminal like *Woodwardiella* in its own line of megascolecine evolution now (Gates, 1958b) has lost some of its morphological and phylogenetic heterogeneity in the same way. *Megascolex* is penultimate in its line of evolution but has, like its ancestor *Notoscolex*, endemic species only in South India-Ceylon and Australia, with or without New Zealand. A classical genus which is only one step removed from the parent of all octochaetines had endemic

species only in New Zealand and peninsular India. To account for those distributions Michaelsen first postulated separate land bridges, from Australia and from New Zealand to India, and later invoked Wegenerian association of continental land masses. Independent origin of identical genera since the Cretaceous was Stephenson's explanation. *Octochaetus* was subsequently split into two subgenera, that were later raised to generic status, but the neoclassical *Octochaetoides* probably still requires (Gates, 1958b) subdivision. Resolution of the notorious and somatically indicated polyphyly of *Notoscolex* and *Megascolex* can be expected with confidence. In the Megascolecidae few genera will be retained, just as in the classical system; one such may be *Diplocardia;* another — the largest of all earthworm genera — is *Pheretima.* Yet, even in *Pheretima,* as already suggested, all genital organs except ovaries, oviducts and cocoon-secreting clitellum can be eliminated within a species, while other structure remains constant.

The wide oceanic discontinuities in distribution, that are so common in the Megascolecidae, characterize several genera of other earthworm families. The Moniligastridae has no such discontinuities, but genera as well as species are distinguished almost entirely by genital characters. Two genera of the little studied Glossoscolecidae provide some evidence (Gates, 1958a) of rapid evolutionary modification in genitalia. In the Lumbricidae, intermediate forms between most of the classical genera long have been known. A recent examination of a couple hundred specimens of an infrequently seen form (Gates, 1957a, p. 13) provided noteworthy instances of individual variation only with respect to those genital characters most used for defining and distinguishing species. In another lumbricid, all genital organs, except as in the above-mentioned pheretimas, have been eliminated, while other anatomical features remained constant. Most lumbricid genera appear (Gates, 1956a, p. 30) "to be only congeries of species associated because of relatively unimportant or superficial convergences." So little is known about so much of the taxonomically important structure in so many species, that *ex tempore* transfers from one polyphyletic genus to another (Gates, 1956a, p. 26) seem inadvisable. The somatic anatomy of various unmentioned subfamilies and families, as

well as of the Glossoscolecidae, certainly is much less known than that of the Lumbricidae.

There is then little to indicate that other earthworms may have been classified, except perhaps by accident, more naturally than the megascolecids. The revision that is needed, throughout the megadrilous portion of the Oligochaeta, may have to be drastic.

Since 1900, one family and two subfamilies (see explanatory notes 7-9, following Table 2), several genera and many species have been erected. Of the latter, the number in *Pheretima* and *Dichogaster* already had been doubled (to *ca.* 300 and 160) by 1930. Many species still are known only from descriptions of a very short series, or of a single type, that sometimes has been aberrant. Little information about reproduction (whether sexual or parthenogenetic), individual and geographic variation has been recorded. Somatic anatomy, rather generally, is too inadequately characterized to permit grouping species according to over-all similarity. Until that information is available polyphyletic taxa cannot be made monophyletic with certainty by any reshufflings based on the literature.

Earthworms have been systematically collected in few areas, even in those immediately surrounding or easily accessible from museum and university centers. Such material as still may be available[5] in institutions usually is the casual spoil of other activities, almost always hastily preserved in the field, often more or less macerated, but if not, probably deteriorating slowly because methods of retaining specimens in good condition are unknown. Even the best of field-preserved material cannot be expected to provide all of the information that is needed, especially with regard to vascular and excretory systems. Decades must pass, so far as can be estimated from the rate of increase in knowledge during the last century, before data as to neglected portions of digestive and other somatic systems will be sufficient to permit grouping species and genera according to over-all similarity.

The problem to which we now return is that of finding a place for a new genus of unknown affinities in an obviously obsolescent

[5] A list of extant types could not be provided by Michaelsen's own institution as late as 1958.

system, at a time when relationships of earthworms cannot be determined from the literature or from extant collections. In such circumstances changes in the system clearly should be minimal to avoid needless extensions in the future of already complicated synonymies.

Racemose prostates of the pheretima kind are present in genera that belong in a region extending through India, China, Malaysia and Australia, perhaps with some intrusion into New Zealand that is not due to human introductions. As wide oceanic intervals are lacking in that region it is possible that all of the forms under consideration have had a common origin. Accordingly, *Exxus* is assumed to be from the same Australasian region and to belong in the Megascolecinae, which alone contains genera having truly racemose prostates without a central canal. The subfamily, as pointed out long ago, already was undefinable morphologically. It can be defined, by its prostates, if forms with tubular glands, regardless of presence or absence of lateral branches from the axial lumen, are excluded. Mesodermal origin of the prostate, in a group where diagnostic characters are few, appears to be an evolutionary innovation of sufficient importance to justify more than subfamily status. The Megascolecinae of Stephenson (1930), as now restricted, accordingly becomes a family in partial agreement with Michaelsen's (1921, 1929) later proposals.

Genera now excluded from the Megascolecidae are distributed among the other subfamilies, in accordance with precedents set when Stephenson, Michaelsen and Pickford disbanded the Trigastrinae and the Diplocardiinae. Thus, genera with holonephric excretory systems throughout go into the Acanthodrilinae, and meronephric genera go into the Octochaetinae. Each of those two groups of genera seems to be entitled to the same rank as the Ocnerodrilidae, which was separated off some years ago (Gates, 1939b). Such rearrangements, in the neoclassical manner, satisfy Stephenson's criterion of convenience. They permit reference to or discussion of groups, having a limited degree of common morphology, independently of the highly subjective phylogenetic esotery on which the classical system is really based.

The synopsis below summarizes the proposed changes along with brief definitions and generic lists.

A_1. Prostates racemose, of pheretima type, without central canal and presumably of mesodermal origin. MEGASCOLECIDAE. Comprises the following genera, some of them perhaps in part only, *Lampito, Pheretima, Perionyx, Plionogaster, Woodwardiella, Comarodrilus, Notoscolex, Megascolex, Digaster, Perissogaster, Didymogaster, Nellogaster, Tonoscolex, Nelloscolex* and *Exxus.*

A_2. Prostates tubular, with central canal, of ectodermal origin.

B_1. Pre-intestinal region short with latero-esophageal hearts confined to x-xi and intestinal origin in or (usually) anterior to xiv. (Setal arrangement lumbricin. Calciferous glands or epithelial-lined diverticular spaces in thickened esophageal wall, in ix-x. Excretory system holonephric.) OCNERODRILIDAE. Genera as in Stephenson, 1930, except for *Aphanascus* which was united with *Malabaria* (Gates, 1942), *Kerria* and *Curgia* which are now known as *Eukerria* and *Curgiona,* and in addition *Deccania.*

B_2. Pre-intestinal region longer, with intestinal origin in or behind xv and with hearts not confined to x-xi or their homoeotic equivalents.

C_1. Excretory system holonephric. ACANTHODRILIDAE. Genera as in Stephenson, 1930, with addition of *Eodrilus, Parachilota, Diplocardia, Zapotecia* and from the megascolecinae *Diplotrema, Plutellus, Pontodrilus, Diporochaeta.*

C_2. Excretory system meronephric. OCTOCHAETIDAE. Genera as in Stephenson, 1930, with addition from the Megascolecinae of *Spenceriella, Megascolides,* as well as the neoclassical *Wegeneriona, Neogaster,* also *Scolioscolides, Lennogaster, Barogaster, Rillogaster, Priodochaeta, Priodoscolex, Travoscolides,* and *Celeriella.*

The tubular prostates do seem to suggest a closer affinity to each other, than to the Megascolecidae, of the families Ocnerodrilidae, Acanthodrilidae and Octochaetidae, which were all included in his Acanthodrilidae by Michaelsen (1921, 1929). Any attempt at formal taxonomic indication of the relationship, in the present circumstances, scarcely seems worth while. Interposition of suborder and series between order and families, as in Michaelsen's later schemes, still seems, in agreement with Stephenson (1930, p. 719), to be unwarranted by our present knowledge.

TABLE 2. Earthworm families and subfamilies in recent classifications of the Oligochaeta

Michaelsen 1900	Michaelsen 1921	Stephenson 1923	Stephenson 1930	Pickford	Herein Proposed
	Neo-oligochaeta (1)				
Megascolecidae	Megascolecina	Megascolecidae			
Eudrilinae	Eudrilidae	Eudrilinae	Eudrilidae		Eudrilidae
			Megascolecidae	Megascolecidae (2)	Megascolecidae
Megascolecinae	Megascolecidae	Megascolecinae	Megascolecinae	Megascolecinae	
	Acanthodrilidae				
Acanthodrilinae	Acanthodrilinae	Acanthodrilinae	Acanthodrilinae	Acanthodrilinae	Acanthodrilidae
Trigastrinae	Trigastrinae (6)				
Diploeardiinae	Diplocardiinae	Diplocardiinae	Diploeardiinae (6)		
Octochaetinae	Octochaetinae	Octochaetinae	Octochaetinae	Octochaetinae	Octochaetidae
Ocnerodrilinae	Ocnerodrilinae	Ocnerodrilinae	Ocnerodrilinae	Ocnerodrilinae	Ocnerodrilidae (3)
	Lumbricina	Lumbricidae			
Lumbricidae	Lumbricidae	Lumbricinae	Lumbricidae		Lumbricidae (7)
Glossoscolecidae			Glossoscolecidae		
Glossoscolecinae	Glossoscolecidae	Glossoscolecinae	Glossoscolecinae		Glossoscolecidae
Hormogastrinae	Hormogastridae	Hormogastrinae	Hormogastrinae		Hormogastridae
Microchaetinae	Microchaetidae	Microchaetinae	Microchaetinae		Microchaetidae
Criodrilinae	Criodrilidae	Criodrilinae	Criodrilinae		Criodrilidae
	Sparganophilidae	Sparganophilinae	Sparganophilinae		Sparganophilidae
	Phreoryetina				
		Moniligastridae	Moniligastridae		
Moniligastridae	Moniligastridae	Moniligastrinae	Moniligastrinae		Moniligastridae (4)
	Syngenodrilidae	Syngenodrilinae	Syngenodrilinae	Syngenodrilidae (5)	
Alluroididae	Alluroididae	Alluroididae	Alluroididae	Alluroididae	Alluroididae (5)
Haplotaxidae	Phreoryetidae	Haplotaxidae	Haplotaxidae	Haplotaxidae	Haplotaxidae

(1)-(9) refer to explanatory notes.

EXPLANATORY NOTES

(1) Suborders of the 1921 scheme, the Archioligochaeta and Neo-oligochaeta, were abandoned in 1929. The suborders then proposed are three, Oligochaeta plesiopora, prosopora and opisthopora.

(2) Pickford, 1937.

(3) Gates, 1939, 1942.

(4) Gates, 1945. In this article, an editor made the author say (p. 394) "Hearts of vi and vii connect the dorsal and ventral trunks to a longitudinal vessel that appears to be an extra-esophageal," which is incorrect and unfortunately was repeated (Pickford, 1945) in a formal redefinition of the Syngenodrilidae. The "hearts," so far as could be determined from the available material, connect the dorsal and ventral trunks only. Another editorial change was deletion of a statement to the effect that the "hearts" are median to the extra-esophageals. Those trunks, so far as is known and except in *Syngenodrilus* and the Monoligastridae, are median to hearts and segmental loops. The pair of characters, lateral to or median to the hearts and segmental loops, eventually will prove to be of considerable taxonomic importance.

(5) Pickford, 1945. Also *cf.* Gates, 1945. Recognition of a family, or even a subfamily, for *Syngenodrilus* alone, at present scarcely seems warranted from, quoting Stephenson, the point of view of convenience or by our knowledge of relationships.

(6) The Trigastrinae of 1900 and 1921 disappeared when Stephenson transferred the Indian *Eudichogaster* (which had been split off from the Afro-American *Dichogaster*) to the Octochaetinae, *Trigaster, Eutrigaster, Dichogaster* and *Monogaster* to the Diplocardiinae. Michaelsen (1933) suggested transfer from the Diplocardiinae to the Octochaetinae of the meronephric *Trigaster, Dichogaster* (presumably including *Eutrigaster*) and *Monogaster*. Genera still left in the Diplocardiinae, the holonephric *Diplocardia* and *Zapotecia*, were placed by Pickford (1937) in the Acanthodrilinae.

(7) The Criodrilinae of 1900 became monogeneric by erection of a family for *Sparganophilus*, transfer to the Microchaetinae of the African *Alma* as well as the American *Drilocrius* (split off from *Criodrilus*).

Pop (1949) included *Criodrilus* in the Lumbricidae without subfamily divisions. Omodeo (1956) excluded *Criodrilus* and recognizes two subfamilies, Lumbricinae and Eiseninae.

(8) The monospecific Hippoperidae was erected (Taylor, 1949) for a eudrilid supposedly distinguished from the rest of the family by presence of a second pair of male pores.

(9) Megascolecid subfamilies are reduced to two in a publication (Lee, 1959) received after the manuscript of this contribution had been typed.

Acanthodrilinae. "One pair of prostatic pores on xvi (rarely) or xvii or xix, or two pairs on xvii and xix (rarely the two pairs may be further back); one pair of male pores, usually on xviii, sometimes on neighbouring segments, sometimes combined with a pair of prostatic pores (in which case, never on xviii); prostates with unbranched central canal." Comprising *Acanthodrilus, Microscolex, Rhododrilus, Dinodriloides, Pericodrilus, Maoridrilus, Neodrilus, Plagiochaeta, Chilota, Yagansia, Udeina, Eodrilus*, the diplocardiine *Diplocardia, Zapotecia, Trigaster, Eutrigaster, Dichogaster, Monogaster*, the octochaetine *Howascolex, Octochaetus* (including *Octochaetoides*), *Dinodrilus, Hoplochaetina, Ramiella, Eudichogaster, EUTYPHOEUS, Hoplochaetella*, the neoclassical *Leucodrilus, Decachaetus, Eudinodriloides, Sylvodrilus* and *Neochaeta*, the Ocnerodriline *Maheina, Curgiona, Malabaria, Paulistus, Eukerria, Kerriona, Haplodrilus, Ocnerodrilus, Pygmasodrilus, Nematogenia*, as well as *Nelloscolex, Tonoscolex, Rillogaster* and *Lennogaster*.

Megascolecinae. "One pair of prostatic pores and one pair of male pores on xviii (*Diplotrema* only) or one pair of combined male and prostatic pores on xviii; prostates with unbranched or branched central canal." Comprising *Diplotrema, Plutellus, Pontodrilus, Woodwardiella, Comarodrilus, Megascolides, Spenceriella, Notoscolex, Megascolex, Pheretima, Plionogaster, Digaster, Perissogaster, Didymogaster, Diporochaeta, Perionyx*, the ocnerodriline *Quechua* (should be *Quechuona*), as well as *Barogaster, Priodochaeta, Priodoscolex, Travoscolides* and *SCOLIOSCOLIDES*. The ocnerodriline *Gordiodrilus* and several neoclassical genera were not placed.

These changes, like others in the neoclassical manner, are not based on any substantial increase in knowledge of somatic anat-

omy. Similarity, for each subfamily, is restricted to presence or absence of united male and prostatic pores in xviii only (megascolecin terminalia). Elucidation of the relationship between *Eutyphoeus* and *Scolioscolides* showed conclusively that the two subfamilies cannot be so distinguished. Further proof probably will be provided by the ocnerodriline genus (*Gordiodrilus*) that could not be placed in either of the revised units. Branching of a central prostatic canal was recorded in some species of *Diplocardia* more than sixty years ago. A central canal is lacking in the prostates of *Nelloscolex* and *Tonoscolex*. *Quechuona* has a short pre-intestinal region (with hearts in x-xi only) such as is characteristic of nearly all ocnerodriles. The megascolecin male terminalia probably are present in *Gordiodrilus*, which clearly belongs in the same family with *Quechuona* and other ocnerodriles.

SUMMARY

In the "classical" system of the Oligochaeta, species are museum taxa, i. e., based on resemblance in a few macroscopically recognizable characters to a type specimen that sometimes was quite abnormal. Information as to individual and geographical variation usually is lacking. Genera, defined by a very few "key" characters and often obviously polyphyletic, are arranged in larger units according to a phylogenetic esotery. Definitions of subfamilies and families are statements of range of variation in certain characters most of which are used to define genera. The system is artificial and obsolescent. Revision of genera on a basis of over-all similarity of species is impossible because of absence in the literature of information about much somatic anatomy. Material needed for adequate characterization of the species (many without types) is unavailable in institutions and is unlikely to be secured for many years to come. To accommodate *Exxus wyensis*, the Megascolecidae of the latest monograph on the Oligochaeta is redefined to include only genera having racemose prostates of the pheretima sort. Excluded species with holonephric and meronephric excretory systems respectively are transferred to the Acanthodrilidae and Octochaetidae.

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